

Notes and Bibliography on the Larvae of Xanthid Crabs¹

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A. Notes on Larvae of Crabs of the Family Xanthidae

DECAPOD SYSTEMATICS have rarely attempted to draw supporting evidence from the larval phase (Gurney, 1942, p. 12). However, it is generally recognized that phylogenetic conclusions drawn from larval stages alone without reference to adult systematics can be very misleading, but the two approaches considered together can be of value. This is especially so in the decapod Crustacea, both in the separation of closely allied species and in the assessment of relationships at all levels. Nevertheless, there are several exceptions to this generalization, more especially in the Caridea where some closely related genera possess widely differing larvae (Gurney, 1942, p. 15).

Among the Brachyura, larval characters are usually more reliable, and most species will possess characters shared by all other species within a given genus. Similarly, generic larval characters usually vary only within limits which determine the brachyuran family to which a genus belongs (see Lebour, 1928). The larvae of a sufficient number of brachyuran genera and species are now known for considerable confidence to be given to the view that if a larva departs significantly from a family or generic type it is unwise to dismiss this fact as irrelevant.

In brachyuran development the pre-zoea and zoea larval stages are considered to be of phylogenetic significance (Lebour, 1928; Gurney, 1942). More importance has been attached to the zoea than to the pre-zoea larval stage, as the zoea larvae are more widely known and more readily observed in the laboratory. The megalopa larva is more properly considered as a post-larval stage (Gurney, 1942) and its significance as an aid to classification is limited

by the small number of genera in which megalopa larvae are known.

Hyman (1925, p. 2) was the first author to recognize a division within the Xanthidae based on zoea larval characters. He divided larvae described up to that time into two groups: (a) those with the antennal exopod minute (*Xantho*, *Panopeus*, *Eurypanopeus*, *Neopanope*), and (b) those with the antennal exopod present as a distinct segment (*Menippe*, *Eriphia*, *Pilumnus*, *Trapezia*).

Lebour (1928) described the larval stages of three British xanthid crabs and noted that Hyman's observations were also true of the British species. Lebour characterized all known larvae of the family Xanthidae and pointed out their affinities with other described larvae of the Brachyrrhyncha, but no further significant conclusions were drawn at this time.

Aikawa (1929, 1933, 1937) used zoea larval characters to formulate a system of classification divorced from that of the adults. In the group "Xanthozoea," *Planes*, *Pachygrapsus* (Grapsidae) and genera of the family Ocypodidae are included together with *Xantho* and the Panopean genera, while *Menippe*, *Eriphia*, and *Sphaerozoeus* are placed in the group "Grapsizoea" (see Aikawa, 1937, pp. 157-158). In the opinion of Gurney (1942, pp. 270-271) these heterogeneous larval groupings serve little purpose and throw little or no light upon adult systematics.

Gurney (1938) and Lebour (1944) both pointed out that groupings of primary larval characters usually sufficient to separate families and genera within the Brachyura did not apply in the family Xanthidae. These conclusions were based on zoea larvae described from 14 genera representing six of the eight subfamilies classified according to Balss (1927).

Since 1944 the zoea larvae of many more species have been described from 14 additional genera. In only a few of these have the pre-zoea and megalopa larvae been discussed.

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However, sufficient data are now available to permit a review of the significance of larval characters found within this large and complex family at a time when adult systematics are in a state of flux.

DIAGNOSTIC CHARACTERS OF KNOWN XANTHID LARVAE

Pre-zoea Larvae

Lebour (1928) considered that all pre-zoea larvae of the family Xanthidae shared the following characters:

- a. Four processes on antennal exopod
- b. Telson with 7+7 posterior processes; outer process smooth (a character then common to all Brachyryncha)

Review of these characters in the light of recent work shows that there are four plumose processes arising from the antennal exopod in all pre-zoea larvae described other than in *Pilumnopus serratifrons* (Kinahan) which has two plumose processes only (Wear, 1968).

The pre-zoeal telson bears seven pairs of posterior processes, but since 1928, only *Chlorodopsis spinipes* (Heller) and *Trapezia cymodoce* (Herbst) have been described as having the first (outer) process smooth (Gurney, 1938) to conform with the British Brachyryncha. Among xanthid crabs there are now six species representing the genera *Cycloxanthops*, *Panopeus*, *Menippe*, *Ozius*, *Heteropanope*, and *Pilumnus* which are known to have this outer process plumose as in *Ebalia* and the Oxyryncha (see Wear, 1968). Hence the presence of a smooth outer process is not a reliable character of pre-zoea larvae of the family Xanthidae or of the Brachyryncha.

Zoea Larvae³

Zoea larval characters of the family Xanthidae given by Lebour (1928) are listed below and evaluated in the light of all xanthid larvae described up to the present time.

- a. Four zoeal stages
- b. Carapace with dorsal, rostral and one pair of smaller, lateral spines
- c. Antenna with vestigial exopod or with exopod nearly as long as the spinous process
- d. Abdomen with lateral papillae (knobs) on somites 2 and 3; somites 3 to 5 (sometimes 6) with lateral spines
- e. Telson cornu with three lateral spines or with one of these tending to disappear in later stages

The number of zoeal stages in the Xanthidae is quite firmly established as four. However, Porter (1960) described six stages for *Menippe mercenaria* Say, but considered that probably only five true stages exist. These observations were based on larvae reared in the laboratory, and the zoeal stages obtained were not compared with natural planktonic stages. *Heterozius rotundifrons* A. Milne Edwards has only two zoeal stages (Wear, 1968), but this species is placed only provisionally in the family Xanthidae.

The majority of known xanthid zoea larvae have four carapace spines. Exceptions occur in only three genera. Gurney (1938) noted the presence of a pair of accessory lateral spines in the first zoea of *Tetralia glaberrima* (Herbst). *Heteropanope glabra* Stimpson (Aikawa, 1929) and *Pilumnopus indicus* (de Man) (Takeda and Miyake, 1968) both possess a dorsal carapace spine but no lateral spines or rostral spine, while *P. serratifrons* has dorsal and lateral carapace spines but only a vestigial rostral spine (Wear, 1968).

The division of xanthid zoea larvae into two groups as based on the character of the second antenna by Hyman (1925) was followed by Lebour (1928). Lebour suggested that *Eriphia* and *Menippe*, which possess an antennal exopod developed to about three-quarters the length of the spinous process, should form a third group situated between *Pilumnus* on one hand and *Xantho* on the other. From all available evidence, the development of the antennal exopod in relation to that of the spinous process still effectively separates two major groups of larvae within the family Xanthidae.

Lateral papillae ("knobs": Lebour, 1928)

³ Characters of all zoea larvae so far described from crabs of the family Xanthidae are summarized in a table contained in the author's Ph.D. thesis held in the library of Victoria University of Wellington, New Zealand.

are known to occur on the second abdominal segment of all brachyuran zoea larvae. In the Xanthidae, papillae are usually present also on the third abdominal segment (Lebour, 1928). However, more recent work shows that the posterior pair of papillae may be absent. Lateral spines on the third to fifth abdominal segments is also a variable character, but these occur in the great majority of xanthid larvae.

The possession of one dorsal spine and two lateral spines on the telson cornu is the last of Lebour's xanthid zoea larval characters listed above. However, it is now known that one or two pairs of these spines may be absent or much modified as in the genus *Ozius* (Wear, 1968), while in the first zoea of *Menippe rumphii* (Fabricius) all three pairs of spines are absent (Prasad and Tampi, 1957). The presence or absence of these spines, therefore, is a character useful only in distinguishing species, or occasionally genera.

Thus the characters given by Lebour (1928) are variable and are of no value in separating zoea larvae of the Xanthidae from those of other brachyrhynchous families, except perhaps the Pinnotheridae. As a group, xanthid zoea larvae conform with Lebour's characters in a very general way, but the larvae are nevertheless similar to those of other brachyrhynchous crabs. From the larval evidence it is not possible to suggest more precise phylogenetic relationships. However, within the family Xanthidae, zoea larval characters are of considerable significance, and they separate the species effectively and distinguish major groups of genera. The most important single character is the length of the antennal exopod in relation to that of the spinous process.

Megalopa Larvae

Lebour (1928) considered megalopa larvae of the family Xanthidae to possess the following characters:

- a. Rostrum pointed and bent or rudimentary
- b. 1st pereopod with a hook on the ischium
- c. Dactylus of 5th pereopod with long setae (feelers) which are common to all Brachyrhyncha except the Pinnotheridae

Review of the literature indicates that Le-

bour's characters of xanthid megalopa larvae do not apply to all species. There is no character which can be used safely beyond the level of genus, but exceptions occur more rarely than among the zoea larvae. The megalopa larva of *Heterozius rotundifrons* departs more significantly from these characters than that of any other species described, and this evidence supports the suggestion that the species does not belong to the family Xanthidae (see Wear, 1968).

REMARKS AND SUMMARY

Zoea larvae of xanthid species whose development is known represent 28 genera, and these fall into two groups based on the ratio of the antennal exopod to the spinous process. The first group is composed of genera included in the subfamily Xanthinae as reconstituted by Balss (1957). These larvae possess a vestigial antennal exopod. Two species which do not have this larval character are *Panopeus bermudensis* Benedict and Rathbun and *P. parvulus* H. Milne Edwards described by Lebour (1944). Their larvae have the antennal exopod and spinous process equal in length, as in the second group, suggesting that these species may not be properly referred to the genus *Panopeus*. There is no larval evidence to support separation of the "Panopean" genera from the "Xanthian" genera as implied by Monod (1956).

The second group is formed by larvae of genera classified in the subfamily Menippinae (Balss, 1932, 1957) and the subfamilies Pilumninae and Trapeziinae as in Balss (1957). Zoea larvae of species and genera in this section are characterized by the presence of a well-developed antennal exopod. There is no larval evidence to suggest a clear distinction between genera in the subfamily Pilumninae and those in the Menippinae. *Heteropanope* and *Pilumnopus* fall into the second group based on the zoeal second antenna, but their larvae lack rostral or lateral carapace spines and therefore warrant distinction as a third larval type within the family Xanthidae.

The above arrangement of genera into two groups bears out a division of the Xanthidae into the Hyperolissa (subfamily Xanthinae)

and Hyperomerista (subfamilies Menippinae, Pilumninae, and Trapeziinae). It will be of considerable interest to see if this holds good for xanthid larvae described in future work.

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B. Bibliography of the Larvae of Crabs of the Family Xanthidae

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- megaloopa of *Pilumnus birtellus* (L.); p. 173: 4 zoeal stages of *Eriphia spinifrons* (Herbst); p. 177: first and second zoeal stages of an unidentified xanthid.]
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